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BIOLOGICAL BULLETIN

EXPERIMENTAL CONTROL OF MORPHOGENESIS IN THE REGULATION OF PLANARIA.

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The present paper is a brief account of certain results of experimental work upon *Planaria* which has extended with interruptions over the last ten years. The data presented here concern *Planaria dorotocephala* Woodworth, but *P. maculata* is similar in most respects. A complete account of the work will appear elsewhere.

I. THE DOMINANCE OF THE ANTERIOR REGION IN REGULATION.

My experiments support very positively the conclusion that in *P. dorotocephala* the anterior region, and more specifically the head region, controls the process of regulation in regions posterior to it and within a certain distance, *i. e.,* it is physiologically dominant over these regions. A limit of effectiveness for this dominance exists and this varies in general with the rate or intensity of the processes in the anterior region. Moreover, not only is the head region dominant over the regions posterior to it and within the limit of effectiveness, but in general a given level of the body is dominant over regions posterior to it within the limit and is dominated by regions anterior to it.

Before considering other facts it is necessary to recall that in nature all asexual individuals of *P. dorocephala* above a certain size consist of at least two zooids and the larger animals of more than two. This is shown by the following facts: (1) If the animals are cut into a series of small pieces of equal length from the anterior end posteriorly, the capacity for head formation decreases and disappears in successive pieces from the anterior end to about the middle of the postpharyngeal region, *i. e.,* the level where fission occurs, and then increases suddenly. This sudden

increase represents the anterior region of the second zooid. Where the second zooid is of considerable length a similar decrease in the capacity for head formation occurs from its anterior end to about the posterior one half to one third of its length, where again a sudden increase in the ability of the pieces to form heads occurs. Posterior to this level there is a more or less diffuse region of very great capacity for head formation probably in reality a series of head regions, extending to the end of the body. Other features of regulation, the rate, the relation between regeneration and redifferentiation, the size of the head and the position of the pharynx show corresponding regional changes. Most of these facts were briefly stated in an earlier paper (Child, '06*b*) and will be considered more fully elsewhere.

Secondly, it is possible by various means to induce fission in a very short time in animals which are far below the size at which fission would occur in nature, or which for other reasons would be incapable of fission under natural conditions. In all cases where fission can be induced it occurs at a level where sudden increase in the capacity for head formation appears. Some of the methods of inducing fission have been described in another paper (Child, '10*b*).

And finally, the length of the second zooid, together with other zooids which may arise from its posterior region varies with the length of the whole, but not proportionally. In very small animals the second zooid cannot be found by any methods thus far employed, but as the animal grows longer, it appears at the posterior end as a short region of high capacity for head formation and as growth continues it increases in length more rapidly than other parts; consequently in very large animals the postpharyngeal region is often double or more than double the length of the prepharyngeal, while in very small animals the prepharyngeal region is the longer. In *Planaria* the second zooid does not develop a head as visibly differentiated region before its separation, as do the posterior zooids of the Microstomidæ and annelids. This is because the processes which make this region morphologically posterior are more firmly fixed in *Planaria* than in those forms. So long as it remains attached to more anterior regions, the development of the second zooid can proceed only

to a certain stage because existing conditions inhibit it. But, as I have pointed out, this development does proceed far enough to permit some degree of independent motor reaction in the second zooid, and it is this which brings about fission.

From the fact of the existence of the second zooid it follows that the region which represents physiologically the posterior end of the first zooid is somewhere near the middle of the postpharyngeal region, or in very large animals, in its anterior third. If we wish to compare anterior and posterior regions of the same zooid, this fact must be kept in mind. Turning now to the question of the dominance of the head region, the facts which indicate this dominance are briefly as follows: A piece above a certain size from any level of the body is capable of reproducing all parts which lie posterior to its level whether it produces a head or not, but it is incapable of giving rise to any of the parts which lie anterior to its level, unless some approach to head formation occurs first.

For example, a piece like *cd*, Fig. 1, is capable of producing a new pharynx and the characteristic postpharyngeal intestinal branches, even though it may fail to form a head, as is the case under certain conditions. On the other hand the piece *ef*, from the postpharyngeal region, *i. e.*, the posterior region of the first zooid, never produces even a pharynx unless some approach to head formation occurs first. If it remains headless as it usually does, it also remains without a pharynx or mouth and no prepharyngeal intestinal region with an axial intestine ever appears. Anterior regulation in such cases is limited practically to closure of the wound.

The dominance of the head region is also clearly shown by the relation between the rapidity of development and the size of the head on the one hand and the position of the pharynx on the other. In pieces from near the anterior end (*e. g.*, *ac* or 12, Fig. 1) the head is disproportionately large and develops very rapidly and the pharynx is situated near the posterior end of the piece (Fig. 3), while in pieces such as *eg*, Fig. 1, from the posterior part of the first zooid, the head is relatively small and forms slowly and the pharynx is anterior to the middle of the piece, Fig. 3. Moreover, it is possible to demonstrate experimentally in pieces
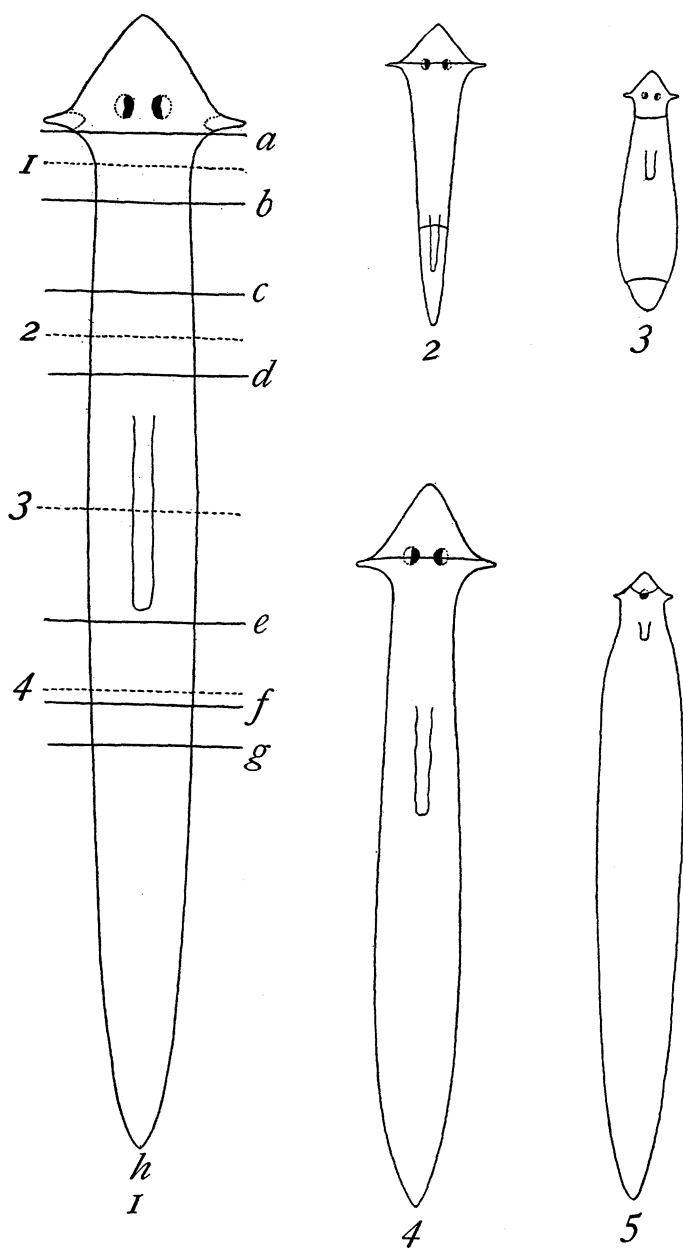
FIGS. 1-5.

from the postpharyngeal region that any external conditions which alter quantitatively the processes which give rise to a head also alter the position of the pharynx.   A single example is given here to illustrate this relation.   The piece *eh*, Fig. 1, including the whole postpharyngeal region and the second zooid, always gives rise, under anything like natural conditions, to animals like Fig. 4 with large heads, normal eyes and the pharynx somewhat anterior to the middle.   If, however, we decrease the rate of the metabolic processes by means of low temperature, anesthetics, CO_2, etc., the head forms much more slowly, remains much smaller, often possessses only a single median eye and the pharynx appears close behind the head and remains of small size.   Fig. 5 shows the position of the pharynx in such a piece after regulation in 1.5 per cent. alcohol, 0.3 per cent. ether or in water containing CO_2. By varying the external conditions quantitatively all gradations between the conditions of Figs. 4 and 5 can be obtained.   Changes in the other direction can be brought about by high temperature and also by other conditions which increase the rate of reactions in the body.   In such cases the head is larger and develops more rapidly and the pharynx lies further posteriorly.

In general I have found it possible by these and other methods to alter the localization of the pharynx in pieces within very wide limits.   Since the pharynx is situated at the posterior end of the median axial intestinal branch of the prepharyngeal region, the localization of the pharynx in the piece is directly related to the length of this axial intestine.   In these experiments a definite spatial relation between the rate of the dynamic processes and the localization and size of organs and regions appears.

Moreover, the dominance of the head region and the limit of its effectiveness also appear in the conditions determining the origin of a second zooid.   In newly hatched *P. maculata*—I have not as yet had opportunity to examine newly hatched *P. doro-tocephala*, but have no doubt that they are similar—the second zooid is not present and even the whole postpharyngeal region is incapable of forming a head when isolated.   In this respect it is like the posterior region of the first zooid in larger animals. As the worm grows longer the capacity to produce a head appears

posterior to a certain level, and once established, the second
zooid grows nore rapidly than the first.   When the animal is
5–8 mm. in length a very short second zooid is present and in
animals sightly longer than this fission may be induced experi-
mentally (Child, '10*b*).   In the posterior region of the second
zooid a third zooid arises early because the head region of the
second zooid is not sufficiently active to control more than a
short region; the extreme posterior region of the body often
seems to consist of a series of very short head regions, reminding
one of the series of minute segments which often appear in
the growing posterior region of various annelids.

Under experimental conditions it is possible to delay or inhibit
the appearance of the second zooid in regulating pieces or to
accelerate it.   For example, if we isolate the region anterior
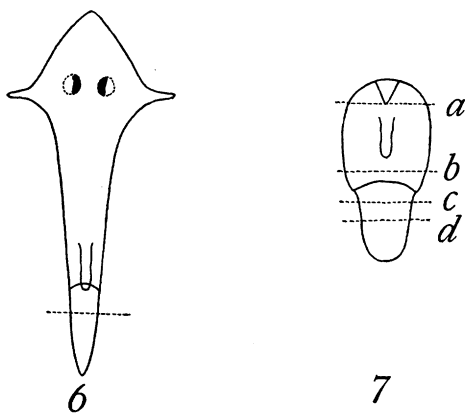
FIGS. 6–7.

to the level *c* or 2 in Fig. 1, including the old head, it forms an
animal more or less like Fig. 6, in which the head and prepharyn-
geal region are disproportionately large.   If now after the growth
and differentiation of the posterior new tissue is completed, we
isolate the posterior end at the level indicated by the dotted line
in Fig. 6, we find it does not produce a new head, *i. e.*, it is physio-
logically as well as morphologically a posterior end.   If we feed
pieces like Fig. 6 so that growth occurs, we shall find that after they
attain a certain length the second zooid appears and after this
the posterior region of the animal shows a high capacity for head

formation.   But such animals must grow to a much greater length
than young normal animals before the second zooid appears,
because in them the dominance of the head region is effective
over a greater distance than in young aninals, and a sufficient
degree of physiological isolation (Child, '10b, '11a) of the pos-
terior region does not occur until a greater length is attained

On the other hand, in pieces of *Planaria* which remain head-
less second, third and further zooids arise at once and if the pieces
can be induced by stimulation to move about sufficiently, fission
often occurs.   The headless piece, unless very small, always
produces a very large amount of new tissue at its posterior end
(Fig. 7).   This new tissue consists of new zooids; if we cut it
off at any of the levels b, c, d (Fig. 7) we find that it always pro-
duces a normal whole very rapidly.   If we remove the anterior
end of the headless piece at the level a in Fig. 7 after the second
zooid has formed at its posterior end we find that it is now capable
of forming a normal head, but this is possible *only when the
second zooid is present,* for if we remove both the anterior end and
the second zooid, the remaining piece is incapable of forming a
head.   This ·last experiment as well as others to be described
elsewhere shows that the second zooid influences regions anterior
as well as those posterior to its anterior end.

In general any condition which retards or inhibits the de-
velopment of the head or the dynamic processes in the developed
head favors the development of a second zooid at the posterior
end and any conditions which accelerate the dynamic processes
in the anterior region retard the development of the second zooid.
As noted above, the length which the animal attains before it
gives rise to a second zooid may also be varied experimentally.
In these experiments we have a demonstration of the spatial
limit of effectiveness of physiological correlation and of the re-
lation between this limit and the rate or intensity of dynamic
processes in the region of origin.

One other point may be added as indicating the dominance
of the head region.   In animals which decrease in size in con-
sequence of starvation the head region decreases less rapidly
than other parts and so becomes relatively larger the further the
reduction proceeds.   Manifestly the head region is able to live

largely at the expense of other parts, to use their substance in maintaining its own structure.

Only a few few brief suggestions as to the occurrence and general significance of dominant and subordinate regions in organisms are possible here. The dominance of the growing tip over other regions in the plant is a well established fact: in my work on *Tubularia* (Child, '07a, b, c, d) I called attention to various facts which indicate that the hydranth region is physiologically dominant over other parts and the same is true for *Corymorpha* and many other, perhaps all hydroids and for all actinians with which I have worked. Moreover, when we recall that in most if not all animals development of the egg begins at the animal pole and that the distal or anterior region arises at or near this pole, the possibility that the "animal" distal or anterior region is very generally dominant becomes at once apparent. I believe that we have here a very general law of development which has not been clearly recognized. It is probable, however, that in many forms the specification of different regions of the egg becomes fixed to such an extent that their further differentiation is to a greater or less extent constitutional rather than correlative, but there are various facts which indicate that within each such "self-differentiating" part we shall find a condition of dominance and subordination of parts more or less similar to that which exists in the whole egg and often even in the adult of some other less highly differentiated forms.

II. The Regulatory Development of the Anterior End.

The "normal" head of *P. dorotocephala* possesses the form shown in Fig. 1. As in various other species of *Planaria* the eyes consist of black pigment spots and unpigmented sensory areas. The sensory cephalic lobes or auricles are also only slightly pigmented and are marked off as well-defined light areas from the rest of the dorsal surface of the head, which is dark brown. The light areas of the eyes and the auricles are indicated in Fig. 1 by dotted lines.

The result of regulation in the larger isolated pieces is usually a "normal whole" (Fig. 4), *i. e.*, and individual with head essentially like Fig. 1, though varying in size, and the other organs

characteristic of the species in nature.   In pieces below a certain size which varies with the region of the body and with other internal and external conditions, normal wholes develop from isolated pieces but rarely or not at all.   A brief description of some of the characteristic results of regulation under these conditions
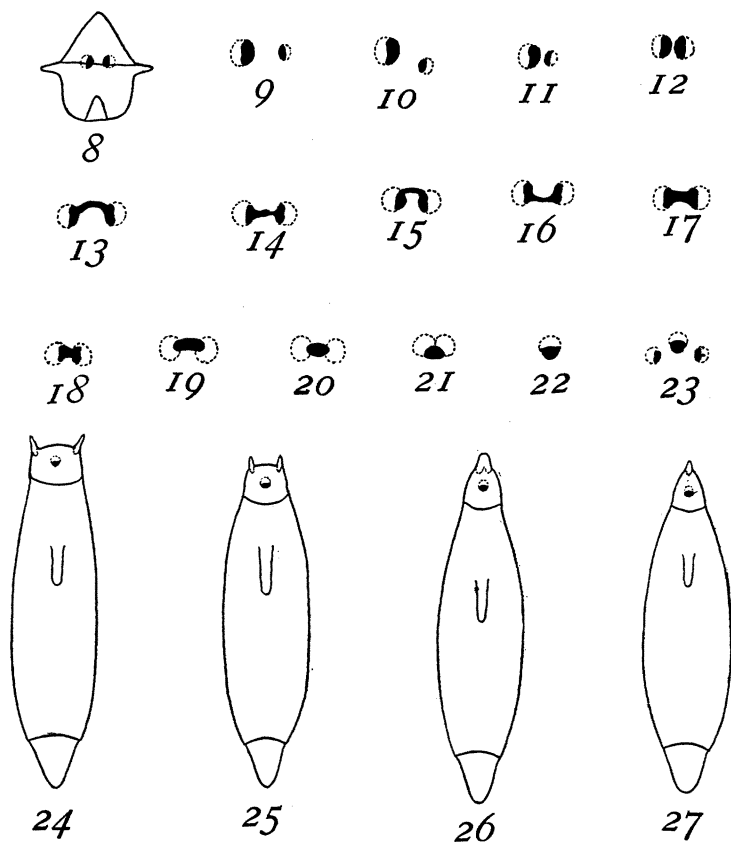
FIGS. 8–27.

is necessary.   For convenience these are arranged under a number of heads, but it must be understood that the "types" thus distinguished are by no means sharply defined.   They grade into each other in various ways, so that the whole series of types is actually a continuous series.

1. *Tailless.*—(Fig. 8.)   Very short pieces from the more anterior regions often give rise, especially under certain experi-

mental conditions to heads without pharyngeal or postpharyngeal regions.

2. *Normal.*—(Figs. 2, 3, 4, 6.)   In larger pieces these are all much alike (Fig. 4), but in smaller pieces they differ according to the region of the body and other internal and external factors.
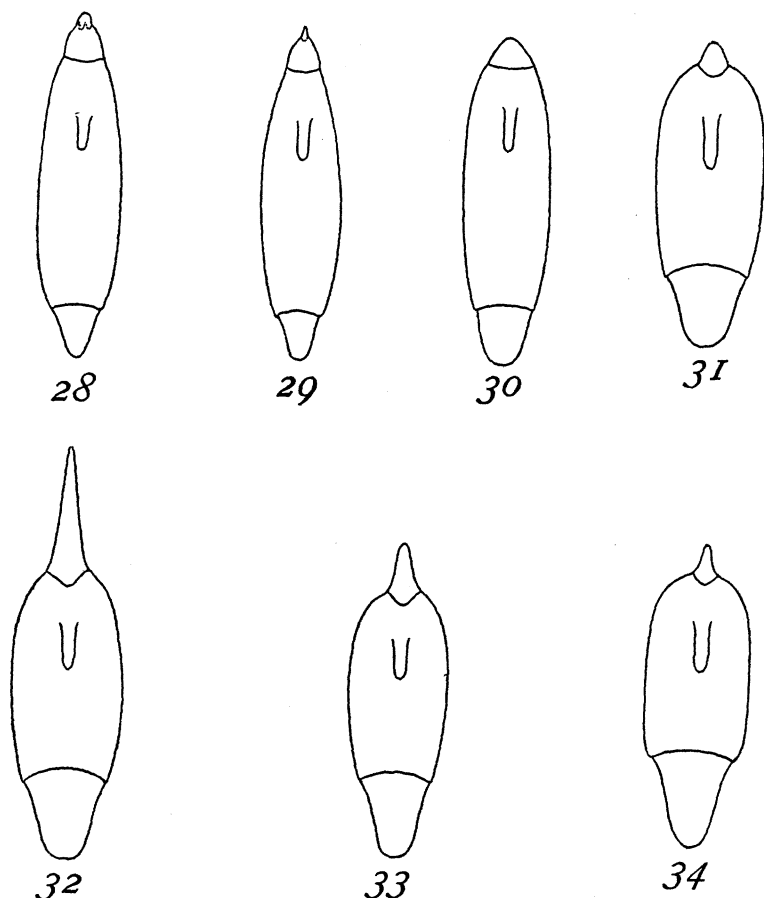
FIGS. 29–34.

Short pieces from the anterior region produce normal wholes like Fig. 2, those above a certain size from the pharyngeal region or immediately posterior to it produce wholes like Fig. 3.

3. *Teratophthalmic.*—(Figs. 9–23.)   Abnormalities of the eyes are frequent in regulation of pieces of *Planaria* and their occur-

rence has been noted by various authors, though no one has previously attempted to determine the conditions of their appearance. They are of various kinds, but in most cases fall into one of the following groups: differences in size or asymmetries of position (Figs. 9–11); approach to the median line (Figs. 11–12) partial union of pigment areas (Figs. 13–19); single median pigment areas with double sensory areas (Figs. 20–21); single median eyes (Fig. 22); three eyes, one median, others right and left (Fig. 23). In all of these cases the head may be entirely normal otherwise, though the more extreme types of abnormal eyes (e. g., Figs. 20–22) usually occur in heads of relatively small size and slow rate of development.

4. *Teratomorphic.*—(Figs. 24–27.) Very frequently, however, the head itself is abnormal in form, the median anterior region being incompletely developed or absent and the auricles appearing on the anterior end of the head and in various degrees of approach to the median line: they may be separated by a considerable interval (Figs. 24, 25), or partially (Fig. 26) or completely united in the median line (Figs. 27). As soon as the new heads become pigmented the unpigmented auricular areas are clearly visible and in such cases as Figs. 26 and 27 it is these areas which enable us to identify with certainty the auricles. Teratomorphic heads almost invariably possess only a single median eye, or they develop a single median eye first and later two more symmetrically placed eyes (Fig. 23); they are always of small size and develop slowly.

5. *Anophthalmic.*—(Figs. 28–34.) These pieces show a distinct outgrowth of new tissue at the anterior end, varying widely in form, but always without eyes. This outgrowth is well innervated and its motor activities resemble those of a head. Sometimes the partially or wholly fused auricles appear anteriorly in the median line on the outgrowth (Figs. 28, 29), as in the extreme type of teratophthalmic pieces (Figs. 26, 27), but usually the outgrowth shows no visible differentiations characteristic of a head. In shape the outgrowth ranges from a broad and blunt form like Figs. 30 and 31 to a very slender form of varying length, often almost as long as the remainder of the piece (Figs. 32–34). These pieces always give rise to a new

pharynx whether they arise from the old prepharyngeal, pharyn-
geal or postpharyngeal regions.

The anophthalmic pieces are always more active than the
headless pieces described below and their movements are better
coordinated; moreover, the motor activity of the anterior out-
growth itself shows very clearly that it represents some approach
to head formation.
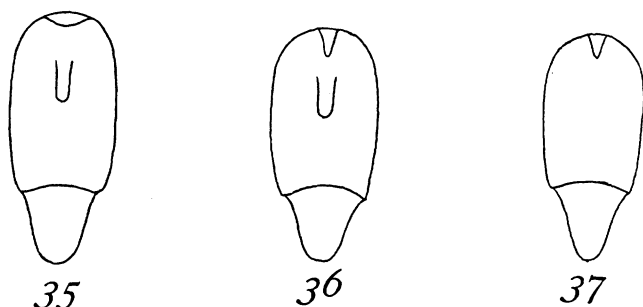
FIGS. 35–37.

6. *Headless.*—(Figs. 35–37.) The headless pieces are dis-
tinguished from the anophthalmic by the fact that the new
tissue merely fills the contracted wound and does not grow out.
According to the degree of contraction of the wound these pieces
may appear like Fig. 35 or Fig. 36. Headless pieces which arise
from the old prepharyngeal or pharyngeal region always develop
a new pharynx (Figs. 35, 36), but these from the postpharyngeal
region do not give rise to a pharynx (Fig. 37).

It will be observed that in the order figured types 2–6 present
a gradation from the normal head to the headless condition.
The eyes first show irregularities, then appear nearer together
and finally in partial or complete fusion in the median line. In
the one eyed forms the region between the auricles may be re-
duced or absent and the auricles appear in various degrees of
approach to each other, or like the eyes partially or wholly
united in the median line, and this latter condition is sometimes
seen in the anophthalmic forms: in these all possible gradations
appear between an outgrowth resembling a head in form to a
long slender pointed outgrowth or one which is short and small,
and finally this condition passes into the completely headless
condition.

The similarity of the first part of this series to the abnormal and cyclopian fish embryos obtained by Stockard is at once apparent.

III. Experimental Control of the Charater of the Anterior End.

Attempts to control the appearance of the various types of anterior end were first made in my experiments some five years ago and it was found that various methods of control were possible. The anesthetics were first used for this purpose almost three years ago; a brief report of certain phases of this work has already appeared (Child, '10*a*). Thus far I have been able to control the process of head formation through various internal and external factors.

In connection with these experiments it has become necessary to standardize the material as far as possible, *i. e.*, to obtain some method of comparing the physiological condition of worms of different size and age, of well fed and starved animals, of animals before and after regulation, pieces from different regions, etc. By the use of alcohol of low concentration (in most cases 1.5 per cent.) I have been able to accomplish this to a considerable extent. A part of the results of this work in their bearing upon the problem of senescence have been described elsewhere (Child, 11*b*). These experiments confirm the conclusion reached from experiments on regulation alone, viz., that in general the capacity for head formation stands in close relation to rate of the metabolic processes in the piece.

For given conditions a certain rate of reaction is necessary for the formation of a normal head. When the rate falls below this critical level teratophthalmic heads appear first, then as the rate falls still further the teratomorphic and anophthalmic and headless forms appear in succession. Moreover, among the teratophthalmic forms the cases of partial fusion represent decrease in rate below the critical level and the single median eyes further decrease. The irregularities of form and position occur most frequently at levels near the old head in small worms and in small pieces from large worms.

Since length of the piece, region of the body and physiological

condition are all factors in the capacity for head formation, pieces which are to be directly compared must be of the same size, except of course where the size factors are under consideration, they must be taken from the same region of the body except where the regional factor is to be analyzed and from individuals in similar physiological condition except where different physiological conditions are being compared. As noted above a relative measure of physiological condition is possible; it is also possible to control the size of the piece and the region of the body from which it comes within certain limits, especially in the pharyngeal region and near the head where localized morphological landmarks exist.

The method of experiment which I have found most satisfactory is to compare considerable numbers of similar pieces rather than individuals. For a temperature experiment for example, animals of the same size and as nearly as possible in the same physiological condition are taken as the basis: from these pieces as nearly as possible of the same size and from the same region of the body are cut and a number, usually fifty, of these pieces is placed in one temperature and a like number in another. For an alcohol experiment fifty pieces obtained in a similar manner are placed in alcohol and fifty in water at the same temperature and under otherwise similar conditions.

By taking into consideration the factors of size of piece and region of the body it is possible to cut series of pieces which will give 100 per cent. or very nearly of normal heads, or on the other hand 100 per cent. or very nearly of headless forms, or we can obtain series which in consequence of unavoidable differences in size and region and differences in the physiological condition of the animals from which they were taken, produce a certain percentage of several of the types described above. In all these cases we can compare the results under the control conditions with those occurring under other definitely known conditions.

For example, pieces above a certain size from the anterior region of the body, which give 100 per cent. or nearly of normal heads in well aerated water at a temperature of 20°C. show a large percentage of teratophthalmic forms in water at 10°C. or in

water containing CO_2 or in alcohol 1.5 per cent. at the same temperature as the control, and under more extreme conditions the teratomorphic, anophthalmic and headless forms appear.

On the other hand, if we take pieces which show nearly 100 per cent. of headless forms in well aerated water at 20° C. we find that similar pieces kept at 30° C. will produce not only anophthalmic, teratomorphic and teratophthalmic heads, but a considerable percentage of normal heads. These illustrations will serve to indicate the general character of the experiments along this line.

Below are given the results of a few series of experiments on size, region, temperature, alcohol, nutrition and mechanical stimulation.

1.   Size and Region.

We may investigate these factors by cutting the whole body of worms of the same size and similar condition into one-fourth, one-sixth, one-eighth, one-twelfth and one-sixteenth pieces, etc., and comparing the results. The following table is a part of a series of this kind and shows in somewhat abbreviated form the results for one-eighth and one-sixteenth pieces of large worms. The head is not included and the pieces of the body are numbered consecutively 1, 2, 3, etc., from the anterior end backward; the consecutive numbers in the second column refer to the pieces. The remaining columns show the percentages of each of the regulatory types for each set of pieces. In this series each set consisted of only ten pieces, but the results are almost as uniform as in much larger series.

In this table the factors of size and region appear clearly. We see that the capacity for forming normal wholes decreases posteriorly and then in the region of the second zooid increases again suddenly. The anterior ends of the one-eighth pieces respectively are at approximately the same levels as those of nos. 1, 3, 5, 7, 9, 11, 13, 15 of the one-sixteenth pieces and it is at once evident that the longer one-eighth pieces possess a greater capacity for head formation than the shorter one-sixteenth pieces.

We can obtain a more striking expression of this fact by comparing very long and very short pieces from similar worms cut with anterior ends at the same level. One of my series of this

		Tailless Heads.	Normal Wholes.	Teratophthalmic and Teratomorphic.	Anophthalmic and Headless.	Dead.
One-eighth Pieces.........	1		100			
	2		10	90		
	3			20	80	
	4			10	90	
	5			10	90	
	6		10	20	70	
	7		80	20		
	8		90	10		
One-sixteenth Pieces.........	1	70	30			
	2		30	60	10	
	3		10	30	60	
	4		10		80	10
	5				100	
	6				100	
	7				100	
	8				100	
	9				80	20
	10			10	70	20
	11				70	30
	12			20	60	20
	13		20		60	20
	14		40		50	10
	15		80	10	10	
	16		90	10		

sort is as follows: from large worms of equal size and similar conditions fifty pieces were cut including the whole postpharyngeal region (*eh*, Fig. I); a second set of fifty short pieces from the anterior end of the postpharyngeal region (*ef*, Fig. I), *i. e.*, with anterior ends at the same level as the larger pieces, was used for comparison. The following table gives the results in percentages.

	Normal.	Teratophthalmic.	Teratomorphic.	Anophthalmic.	Headless.	Dead
Long...............	100	0	0	0	0	0
Short...............	0	0	2	10	82	6

In the same way we may compare other levels of the body and show to what extent the power of head formation depends upon the cells near the anterior cut end and to what extent upon their connection with more posterior regions. My experiments along this line show that in general the ability to form heads in pieces from the posterior region of the first zooid is almost wholly dependent upon their connection with more posterior regions, while in pieces from the anterior end of the body it is very largely independent of such connection.

2. *Nutrition.*

My experiments along this line are rather extensive and the results are of considerable interest. I give here only a single series of experiments. The pieces used included approximately the region between the lines 2 and 3 in Fig. 1; fifty pieces were cut from worms which had been fed every 2–4 days for two months (I), another set of fifty pieces from worms of approximately the same size which had had no food for forty days before the experiment began (II). Results are given in percentages.

	Normal.	Teratoph-thalmic.	Terato-morphic.	Aboph-thalmic.	Headless.	Dead.
I.	4	46	6	30	14	0
II.	0	0	2	10	64	24

The capacity for head formation is manifestly much greater in the well-fed (I) than in the starved pieces (II).

3. *Temperature.*

Under this head only a single series is given, but the results are characteristic. In this series fifty pieces from similar worms including the region between the lines 3 and 4 in Fig. 1 were allowed to regulate at each temperature. Results are given in percentages.

	Normal.	Teratoph-thalmic.	Terato-morphic.	Anoph-thalmic.	Headless.	Head.
28°–30°	74	22	2	0	0	2
18°–20.°	22	40	2	14	22	0

The death of one individual (2 per cent.) at high temperature was purely accidental. The percentages show the general character of the results. With greater differences of temperature greater differences in the results can be obtained.

4. *Alcohol.*

The experiments with alcohol and other anæsthetics present certain complicating factors which will be considered fully elsewhere, but the effect of alcohol upon the capacity for head formation and upon the character of the head formed is readily demonstrated.

In the series presented here fifty pieces from similar worms, including the region between lines 2 and 3 in Fig. 1 were placed

in alcohol 1.5 per cent. for 48 hours after section and then removed to water; fifty similar pieces were placed in water for control. Results are in percentages.

	Normal.	Teratoph-thalmic.	Terato-morphic.	Anoph-thalmic.	Headless.	Dead.
Alc. 48 hrs.........	14	16	8	18	38	6
Water	20	44	2	26	8	0

A much larger percentage of headless forms appears in alcohol than in water.

5. *Complications in the Effects of Depressing Agents and Conditions.*

In the present paper I wish merely to record the fact that under certain conditions and within certain limits depressing factors increase the head-forming capacity in pieces, instead of decreasing it. As I shall show elsewhere, this result can be accounted for without difficulty. It depends largely upon the fact that the rate of metabolism in the cells at the anterior end of the piece which react to the wound increases in the course of this reaction, while that of more posterior regions of the piece remains essentially the same. The depressing factor decreases the rate in both regions and with a certain degree of depression the more posterior region will become almost quiescent while the anterior region which loses its previous differentiation in consequence of the wound reaction will still be active. Under these conditions the dominance of the anterior over the posterior region will be increased and a larger percentage of heads may be formed in spite of the depressing effect, simply because the anterior region is more capable of living, growing and differentiating at the expense of the posterior region. Under these conditions then the depressing effect will appear to be a morphogenic stimulus.

6. *Mechanical Stimulation.*

As is well known, the shorter pieces of the planarian body, especially those from the more posterior regions of the first zooid, very commonly move about but little until regulation has attained a certain stage; after this stage "spontaneous" movements occur. Larger pieces show these movements at

earlier stages and in still larger pieces, *e. g.*, after removal of only the head region, they are never absent. In general the pieces which show more motor activity when left undisturbed in the dishes and which react more readily to slight stimuli are those which have the greater capacity for producing new heads, *i. e.*, for becoming wholes. From a number of pieces it is possible within a few hours after section to select with a considerable degree of certainty those which will form heads, or which will show the greater degree of head forming capacity, merely by observing the differences in motor activity and reaction to slight stimuli.

With these and various other facts in mind I carried out experiments to test the effect of mechanical stimulation to movement upon the formation of heads. The pieces were cut of such size and such distance from the old head that they showed little or no "spontaneous" movement during the first few days after section. Various methods of stimulation were employed: one of these was that of tilting the broad flat dish in which they were kept so that each piece was out of water for a few seconds. This usually serves to induce locomotion, but it does not continue long after the pieces are again in water. Sometimes the pieces were loosened from the glass by currents from a pipette or were turned upon their dorsal surfaces with needles, after which they usually righted themselves. But the most commonly used and most effective method was that of stroking or gently pushing the pieces with a small soft camel hair brush. Usually a few seconds of such stimulation was followed by relatively long sustained locomotion. The stimulation began a few moments after section of the pieces and was repeated at least every hour and often every half hour from about 8.30 A.M. till 6 P.M. and again at least twice between 8 and 11 P.M. each day until the heads in such pieces as produced heads were well developed and the eyes visible. Each time that the pieces of the one set were stimulated the water of the dish containing the control was gently disturbed and stirred in order to avoid as far as possible differences in aeration. Care being taken not to touch the control pieces directly, the movement of the water almost never induced movement of the pieces. The dishes were kept

under as nearly as possible identical conditions of light and temperature.

Two series of experiments are given here. In the first the pieces included the region between the lines 2 and 3, Fig. 1, fifty pieces for stimulation (I) and fifty for control (II) being taken from similar worms.

	Normal.	Teratoph-thalmic.	Terato-morphic.	Anoph-thalmic.	Headless.	Dead.
I.	0	28	8	32	32	0
II.	0	8	8	26	58	0

The second series consists of pieces including the region between the lines 3 and 4 in Fig. 1 and from the same worms as the first. These pieces, being posterior to those of the first series and of approximately the same size produce heads less frequently. As in the first series, fifty pieces were used in the stimulated set (I) and fifty in the control (II).

	Normal.	Teratoph-thalmic.	Terato-morphic.	Anoph-thalmic.	Headless.	Dead.
I.	4	10	2	18	64	2
II.	0	6	2	12	80	0

The two pieces which produced normal heads in the stimulated set of this series were undoubtedly pieces which included the anterior end of the second zooid: the presence of this region even at the posterior end of a piece increases greatly its head-forming capacity. In both series the effect of stimulation appears unmistakably in the increased capacity for head formation. Without doubt it is not the actual performance of the movement itself but the stimulation which is the important factor. Stimulation means increase in the rate or intensity of the dynamic processes in the piece and this appears in increased and altered formative capacity. I believe that these and other similar experiments to be described elsewhere establish and confirm against all objections my position that the process of regulation is essentially a dynamic, or as I have often called it, a "functional" process or complex of processes.

7. *The Morphogenic Effect of Quantitative Changes in Conditions in General.*

In the temperature, nutrition and stimulation series the experimental conditions differ quantitatively from those of the control.

For reasons which I shall state later it seems probable that the factor of length of the piece is essentially quantitative in its effect upon head formation, and the regional factor is certainly very largely quantitative. The effect of alcohol and other anæsthetics is also quantitative, at least in large part.

The results obtained in these experiments point to the possibility of controlling and analyzing morphogenesis in a great variety of ways and of obtaining some insight into the nature of morphogenic processes themselves. As regards the data presented, there are many facts which indicate that the rate of oxidations or of certain oxidation processes is the chief factor in the results obtained.

From the morphological point of view the most important point is that certain organs may alter their localization, their form and their relation to each other and may finally disappear as the rate of the processes concerned decreases and vice versa. It is evident that under given conditions a certain rate of certain dynamic processes is necessary for the production of certain morphological effects.

IV. The Effect of Change of Position of Parts in the Body.

If we cut small pieces from the posterior region of the first zooid such for example as *ef*, Fig. 1, they will give 100 per cent. or nearly of headless forms, If, however, we cut out a large piece, *eh* (Fig. 1) and allow a head to form at its anterior end and then after a week or ten days cut out small pieces just behind the head, we shall find that they now produce 100 per cent. or nearly of forms like Fig. 2, *i. e.*, normal wholes. These pieces represent approximately the region which when taken from the original animal gave rise to 100 per cent. or nearly of headless forms. Their capacity for forming heads has been widely altered by their changed position in the body and more specifically I believe by altered correlation with other parts. The cells of such a region are not directly concerned in the formation of a head, but the more anterior their position in the new individual, the greater their head forming capacity becomes.

In a similar manner we can decrease the head-forming capacity

of parts which were originally near the anterior end and possessed the capacities characteristic of that region. We can make almost any portion of the prepharyngeal region into a pharyngeal region with corresponding change in regulatory capacity. The anterior region of the second zooid, with its very high regulatory capacity may be changed into the postpharyngeal region of a first zooid with a great decrease of regulatory capacity. Changes of this kind may be made almost at will merely by so arranging the experiment that the part in question is brought into a certain position with regard to other parts. It not only acquires a different structure but its capacities are altered. These experiments show a wide range of possibilities of influencing the morphogenic capacities of parts indirectly through correlation. I believe the point is of some general interest. In general terms these experiments show that the regulatory capacity of a part of the body may be altered through correlation. As regards a specific case, the head, they show that a part which when isolated originally possessed little or no capacity to form a head may have this capacity greatly increased by closer association with a region where a head is forming, even though the part itself is not directly concerned in the formation of the head. Such facts as these, possess, I believe, a certain significance in connection with the problem of inheritance. In these cases we actually alter the hereditary capacities of the part in question by altering its correlation with other parts.

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